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Fish Predation Pressure on and Interactions Between Cladocerans: Observations Using Enclosures in Three Temperate Lakes (Germany) and One Tropical Lake (Ethiopia)

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With 10 Figures and 3 Tables

Key words: Cladocerans, enclosure fish predation, temperate lakes, tropical lake

Abstract

Observations were made on the response of cladocerans to fish predation and the interactions among cladocerans using enclosure experiments in three temperate lakes (Germany) and one tropical lake (Ethiopia). In all lakes large-sized cladocerans were removed by fish until small-sized ones and rotifers remained. In apparently all cases the cladocerans of small-bodied species assumed their largest sizes in no-fish enclosures. In fish-enclosures, the small-bodied cladocerans assumed high biomasses due to elevated food resources in the absence of competition from large-bodied cladocerans. It was also observed that in the absence of fish predation, the dominating large-sized species had an excluding effect on other small-bodied cladocerans. In all cases variations between lakes were observed in the behavior of cladocerans even when fishes were absent.

Introduction

Large pigmented and actively moving cladocerans (*Daphnia* spp. in particular) are known to be selectively preyed upon by fish (HRBACEK et al. 1961; BROOKS & DODSON 1965; ZARET 1980). Among these, gravid females are preferred prey, affecting the reproductive rates and biomass of the large-bodied cladoceran species when this is associated with sustained fish predation pressure (GLIWICZ & PIJANOWSKA 1989). In such scenarios the system eventually shifts to domination by small-bodied cladoceran species (VANNI 1987; SLUSARCZYK 1997; BROOK LEMMA 1997). The presence of fish indirectly guarantees the proliferation of small-bodied cladocerans, which are protected from fish predation by their small sizes.

The absence of fish predation is known to stimulate the development of large-bodied cladocerans in which case somatic growth is stimulated at the expense of lengthened reproductive stages (SLUSARCZYK 1997). Essentially, in this inverse scenario of absence of fish predation, the small-bodied cladoceran species are left to compete with the large-bodied herbivorous cladocerans for much of the same size range of the phytoplankton community (BROOK LEMMA 1997).

The investigation of such interactions of different sized cladocerans in the presence or absence of fish predation is of interest since much of biomanipulation depends on them in bringing about reduction in algal bloom. It will, therefore, be attempted in this paper to show the response of different size ranges of cladocerans to fish predation, the interaction between the cladocerans themselves and to show the scenario-differences in four lakes (in one tropical lake and three temperate lakes).

The study sites

The three temperate lakes (Germany)

The three temperate lakes are located in north-eastern Germany in the Brandenburg-Mecklenburg Lake District. Some basic limnological data and the locations of the studied lakes are given in Table 1 and Figs. 1 and 2.

Lake Feldberger Haussee

Feldberger Haussee (also written here as Lake Haussee for short) is an alkaline and highly eutrophic lake. Before 1985, there was an unhindered wastewater inflow into the lake from

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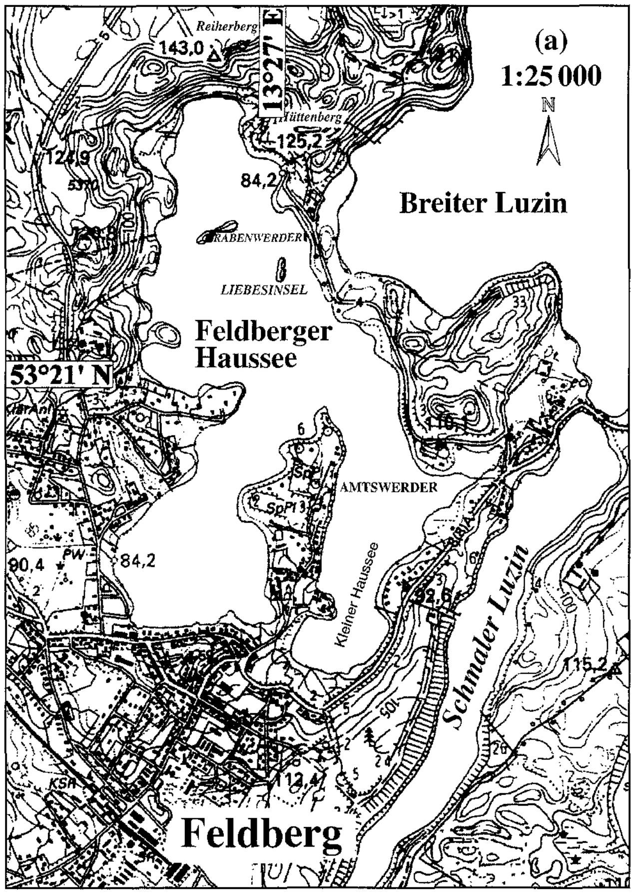
the town of Feldberg (Fig. 1a). Therefore, restoration procedures were initiated (KASPRZAK et al. 1988a; KOSCHEL et al. 1993; RONNEBERGER et al. 1993). In the following years, efforts were made to reduce the predation pressure on macrozooplankton by eliminating planktivorous fish and introducing piscivores (e.g. pike perch) in their stead (KASPRZAK et al. 1993; KOSCHEL et al. 1993). The cladoceran *Daphnia* spp., particularly *D. cucullata*, started to dominate, but the phytoplankton community was replaced by filamentous Cyanobacteria (KRIENITZ et al. 1996).

Lake Große Fuchskuhle

Lake Große Fuchskuhle (also written here as Lake Fuchskuhle for short) is located in an uninhabited forest area south of Lake Stechlin. It is a naturally occurring acidic bog lake used for biomanipulation studies by dividing it into four compartments by plastic walls anchored into the sediment (KASPRZAK et al. 1988b; KASPRZAK 1993). The small size of Lake Fuchskuhle (Fig. 1b), the limited variables of its food web due to lakewater acidity and its isolation of the bog lake from external interference by dense forest provided an ideal condition to conduct controlled experiments (BROOK LEMMA 1997; KRIENITZ et al. 1997). The phytoplankton community is dominated by *Chromulina* cf. *sphaeridia* and *Dinobryon pediforme,* and the zooplankton is dominated by *Diaphanosoma brachyurum* and *Eudiaptomus gracilis* (KRIENITZ et al. 1997). The phantom midge (*Chaoborus*) and waterbugs (Corixidae) are top level predators (KASPRZAK et al. 1988b; KOSCHEL 1995). This study was conducted in the northeastern compartment of Lake Fuchskuhle, which was selected because of its accessibility, plankton structure and composition.

Lake Dagowsee

Lake Dagowsee is also located in the Lake Stechlin area. The eutrophication of this lake dates back to the 1960s when breeding of carp and ducks was carried out in it (KOSCHEL et



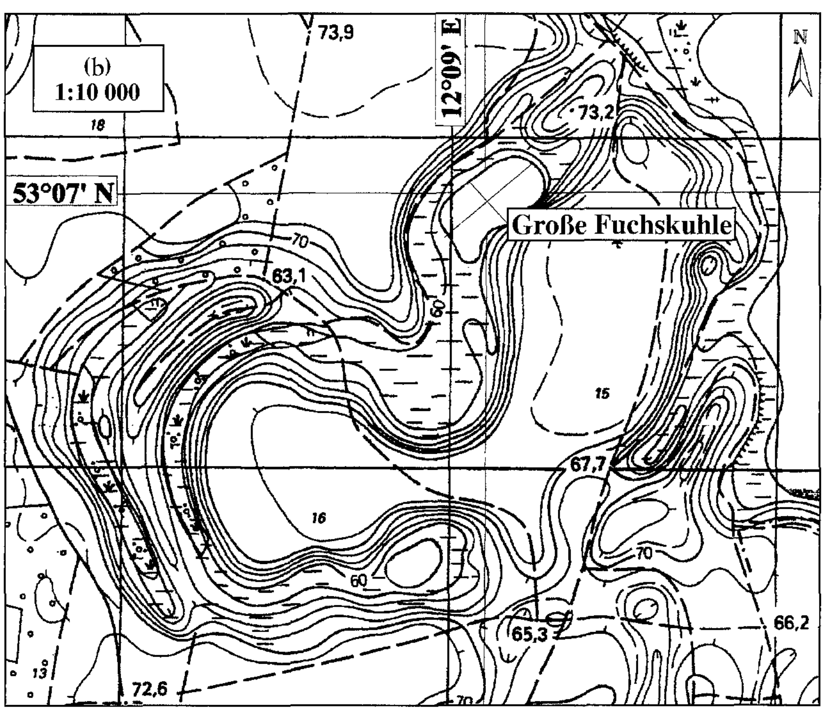


Fig. 1. Locations of Lake Feldberger Haussee (**a**) and Lake Große Fuchskuhle (**b**).

Table 1. Some limnological features of Lakes Fuchskuhle, Haussee, Dagowsee and Kuriftu [after KASPRZAK et al. (1988a[1] & b[2]); KASPRZAK (1993)[3]; BABENZIEN & BABENZIEN (1990)[4]; KOSCHEL et al. (1990)[5]; HEHMANN & KRIENITZ (1996)[6]; BROOK LEMMA (1997)[7]].

Lake features	Lake Fuchskuhle[2,3,4,6,7] (Germany)	Lake Haussee[1,3,5,7] (Germany)	Lake Dagowsee[4,5,7] (Germany)	Lake Kuriftu[7] (Ethiopia)
Location	53° 07′ N & 12° 59′ E	13° 27′ E & 53° 21′ N	13° 04′ E & 53° 08′ N	39° 00′E & 8° 47′ N
Altitude (m)	63.1	84.2	60.2	2000
Area (km^2)	0.015	1.3	0.3	0.4
Max. depth (m)	5.5	12.0	9.5	6.0
Mean depth (m)	2.8	6.0	5.0	2.0
Volume (m^3)	53×10^6	8.2×10^6	1.2×10^6	3.0×10^6
Secchi depth (m)	0.9–4.7	0.95–3.05	1.5–4.7	0.15–0.20
pH[6]	3.8–5.9	8.9	7.2–9.2	7.9–8.4
Cond. ($\mu S\ cm^{-1}$)	60.4	330	340	240
PO_4-P ($mg\ m^{-3}$)	3.1	790 (before 1985) 240 (after 1986)	114	No data

al. 1990). In 1972, with stopping domestic waste inflows and breeding of carp and ducks started a restoration program in this lake (Fig. 2a). In 1993, a pilot project on calcite precipitation, using enclosures, was started with the aim to develop a bottom-up eco-technology for lake restoration (see DITTRICH et al. 1997).

The tropical lake, Lake Kuriftu (Ethiopia)

Lake Kuriftu is an artificial lake, which was filled by diverting runoff in the rainy seasons into an empty crater (Table 1; Fig. 2b). The purpose was to conserve water and to introduce fish as a supplementary protein source to the surrounding population in a country affected by severe water and food shortages. Nutrients enter this lake seasonally with the runoff and through the community activities such as irrigation, animal watering, bathing and washing clothes.

Materials and Methods

A total of four enclosures were made out of 0.1 mm thick clear plastic. They were built into large tubes, each with a diameter of 2 m, a depth of 3.15 m, a volume of 19.8 m^3 and ending with a weighted metal ring at the bottom (RIEMANN & SONDERGAARD 1986; NICHOLLS et al. 1996; PEREZ-FUENTETAJA et al. 1996; RODUSKY & HAVENS 1996). The enclosures were covered at the bottom with a 500 µm mesh-size net to prevent the entrance of fish, fish larvae and invertebrate predators (CHRISTOFFERSEN 1993), but to allow water exchange (ARCIFA et al. 1986). The upper edges of the plastic enclosures were fitted with a 2.5 mm mesh-size net to prevent fish intrusions and the interference of piscivorous birds (CHRISTOFFERSEN 1993; PEREZ-FUENTETAJA et al. 1996). These enclosures were then lowered with the bottom first into

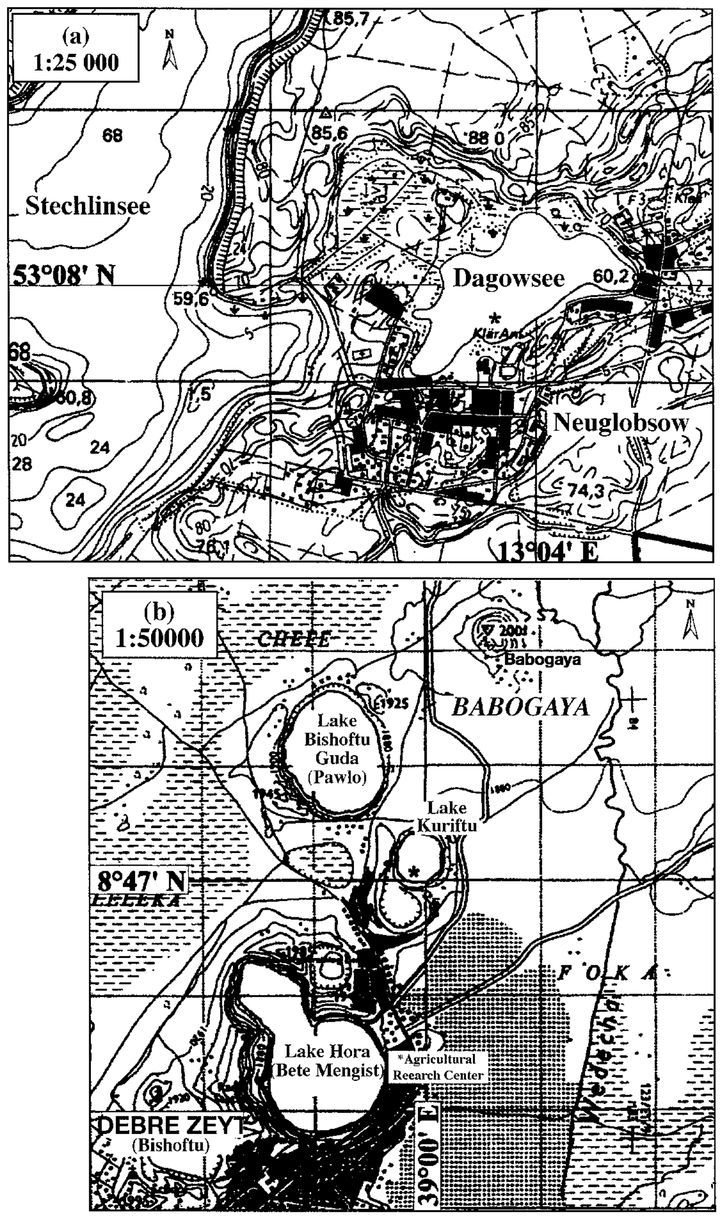


Fig. 2. Locations of Lake Dagowsee (**a**) and Lake Kuriftu (**b**).

the experimental lakes, thus allowing water to fill in upward through the 500 μm mesh. They were left anchored in the lake for 4-6 weeks in June, July and August 1994 and 1995. The dates of the experiments were: in Lake Haussee from 6.6.94 to 12.7.94 and again from 1.8.94 to 22.8.94; in Lake Fuchskuhle from 5.8.94 to 25.8.94; in Lake Kuriftu from 8.12.94 to 29.12.94; and in Lake Dagowsee from 7.6.95 to 5.7.95. Between these experiments, the enclosures were pulled out of the lakes and washed with strong water jet to their original clear transparent state.

At the beginning, all enclosures contained native plankton populations of the respective lakes. The series of experiments in the different lakes were conducted with two enclosures in each lake, where one is designated as no-fish enclosure and the other as fish-enclosure. For comparative purposes with the natural systems of the lakes an additional experiment was conducted in the lakewater very close to the enclosures. Exceptions were made in Lake Haussee where the experiments were conducted twice (each time with two enclosures) and in the last experiment conducted in Lake Dagowsee, where two no-fish enclosures and two with-fish enclosures were used (duplicates). These modifications were made to see if results were reproducible. In all cases, on the first day of the experiment assessment was made to see the initial limnological similarities of the three systems (lakewater, no-fish enclosure and fish-enclosure). On the third day zooplanktivorous fish (*Perca fluviatilis*) with an average individual weight of 5.11 g and a length of 7–10 cm at an average rate of 30 g m^{-2} wet weight were added to the fish-enclosures of the German lakes (RIEMANN & SONDERGAARD 1986; BACA & DRENNER 1995; PEREZ-FUENTETAJA et al. 1996). In the fish-enclosure of Lake Kuriftu (Ethiopia), *Barbus* sp. of similar sizes was used in place of *P. fluviatilis.*

During the experiments in the manipulated enclosures and lakewater water temperature, conductivity, pH and dissolved oxygen were measured using standard WTW field equipment. Integrated vertical zooplankton samples were collected from 3 m up with a zooplankton net of 55 μm mesh-size. The collected samples were immediately preserved by the addition of 4% sugar-formalin solution. Identification, counting and biomass assessments were made by examining a homogenized 1 ml sub-sample in a sedimentation chamber under an inverted microscope (KASPRZAK et al. 1993; RONNEBERGER et al. 1993).

Average body lengths of 20 to 30 individuals of cladocerans from the enclosures and lakewater were recorded to the nearest 1 μm (BØRSHEIM & ANDERSEN 1987; LATHROP & CARPENTER 1992). All measurements from each sample were averaged for each species. Biomass was estimated by calculating cell volume from simple geometric models (BØRSHEIM & ANDERSEN 1987). As much as possible the average deviation was shown in the figures for a better statistical interpretation of the data.

Results

Data with regard to water temperature, conductivity, pH and dissolved oxygen measured in the enclosures and lakewater are given in Table 2. A wide variety of zooplankton species was encountered in the studied lakes (Table 3).

Lake Haussee

A diverse cladoceran assemblage among which *D. cucullata* was the dominant species appeared in the first experiment from 6.6.94 to 12.7.94 (Table 3). The expected differences were delayed for some time apparently due to interference by invertebrate planktivory, presumably, *Chaoborus* sp. or for other unknown reasons. But the biomass and related biological data of *Chaoborus* sp. were not measured. The effect of manipulation started to appear on the third week and continued thereafter. In no-fish enclosure the biomass and body size of *Daphnia* spp. and *Diaphanosoma* sp. were appreciably higher than in the lakewater and with-fish enclosure (Fig. 3). *B. coregoni* showed a conservative pattern by remaining

Table 2. Ranges of some physico-chemical parameters measured at the water surface at the beginning and end of each experiment in the study lakes (LW: Lakewater; NF: no-fish enclosures; WF: with-fish enclosures).

Parameters	Lakes and duration of each experiment					
	Lakewater and enclosures	L. Haussee (Expt. I) 6.6.94 to 12.7.94	L. Haussee (Expt. II) 1.8.94 to 22.8.94	L. Fuchskuhle 5.8. 94 to 25.8.94	L. Dagowsee 7.6.94 to 5.7.95	L. Kuriftu 8.12.94 to 29.12.94
Temp., °C	LW	15.7 to 23.3	27.7 to 18.3	26.2 to 18.6	18.5 to 20.0	20.0 to 19.8
	NF	15.5 to 22.8	27.2 to 18.0	24.9 to 18.9	18.5 to 20.2	21.0 to 19.3
	WF	15.5 to 22.8	27.4 to 18.3	27.3 to 18.8	18.3 to 20.1	21.0 to 20.0
Cond. (Scm^{-1})	LW	326 to 324	293 to 315	38.0 to 40.8	347 to 369	240 to 241
	NF	324 to 317	301 to 316	39.5 to 40.3	349 to 334	245 to 238
	WF	324 to 305	296 to 322	38.6 to 39.8	350 to 355	245 to 240
pH	LW	8.48 to 9.29	8.89 to 8.35	5.24 to 5.20	8.02 to 8.72	7.92 to 8.51
	NF	8.55 to 9.04	8.70 to 8.19	5.14 to 5.14	8.05 to 8.84	8.22 to 8.42
	WF	8.65 to 9.49	8.80 to 7.97	5.24 to 5.23	8.06 to 8.75	8.42 to 8.18
Diss. O_2 (mg l^{-1})	LW	8.9 to 9.8	11.8 to 8.5	5.7 to 9.6	8.1 to 11.8	5.0 to 5.5
	NF	8.9 to 10.0	10.8 to 7.9	4.5 to 9.0	8.2 to 16.8	6.0 to 4.0
	WF	9.5 to 13.8	11.7 to 7.0	5.2 to 9.2	8.3 to 15.2	6.7 to 4.0

Table 3. Zooplankton identified in Lakes Fuchskuhle, Haussee, Dagowsee and Kuriftu.

Groups	Lake Fuchskuhle	Lake Haussee (Expt. 1)	Lake Haussee (Expt. 2)	Lake Dagowsee	Lake Kuriftu
Cladocera	*Daphnia* spp. *Diaphanosoma brachyurum* *Ceriodaphnia* sp. *Bosmina longirostris* *Eubosmina* sp. *Chydorus* sp. *Acroperus* sp. *Pleuroxus* sp.	*D. cucullata* *D. galeata* *D. hyalina* *D. bastard* *D. brachyurum* *B. coregoni* *B. longirostris* *Ceriodaphnia* sp. *Chydorus* sp. *Scapholebris* sp.	*D. cucullata* *D. galeata* *D. hyalina* *D. bastard* *D. brachyurum* *B. coregoni* *B. longirostris* *Ceriodaphnia* sp. *Chydorus* sp.	*D. cucullata* *D. galeata* *D. hyalina* *D. bastard* *D. brachyurum* *B. coregoni* *B. longirostris* *Ceriodaphnia* sp. *Alonella* sp.	*D. barbata* *Moina micrura* *Diaphanosoma* sp. *Ceriodaphnia* sp.
Rotifera	*Keratella* spp. *Polyarthra* sp. *Lecane* sp. *Cephalodella* sp. *Trichocerca* sp. *Filinia* sp.	*Polyarthra* sp. *Keratella* sp. *Lecane* sp. *Proales* sp. *Asplanchna* sp.	*Polyarthra* sp. *Keratella* sp. *Lecane* sp. *Kellicottia* sp. *Proales* sp. *Asplanchna* sp. *Filinia* sp. *Trichocerca* sp.	*Keratella* sp. *Kellicottia* sp. *Brachionus* sp. *Filinia* sp. *Lecane* sp. *Polyarthra* sp. *Asplanchna* sp. *Synchaeta* sp. *Conochilus* sp.	*Brachionus falcatus* *B. calcyflorus* *Synchaeta vorax* *S. pectinata* *Asplanchna* sp. *Lecane* sp. *Polyarthra minor* *Filinia* sp. *Hexarthra* sp. *Conochilus dossaurius* *Euchlanis* sp.
Copepoda	*Eudiaptomus gracilis* *Cyclops* sp.	*E. gracilis* *Cyclops* sp. *Thermocyclops* sp. *Paracyclops* sp. *Metacyclops* sp. *Mesocyclops* sp. *Diacyclops* sp.	*E. gracilis* *Cyclops* sp. *Thermocyclops* sp. *Paracyclops* sp.	*E. gracilis* *Cyclops* sp. *Thermocyclops* sp. *Paracyclops* sp.	*Thermocyclops* sp.
Ciliata	*Stentor* sp.				

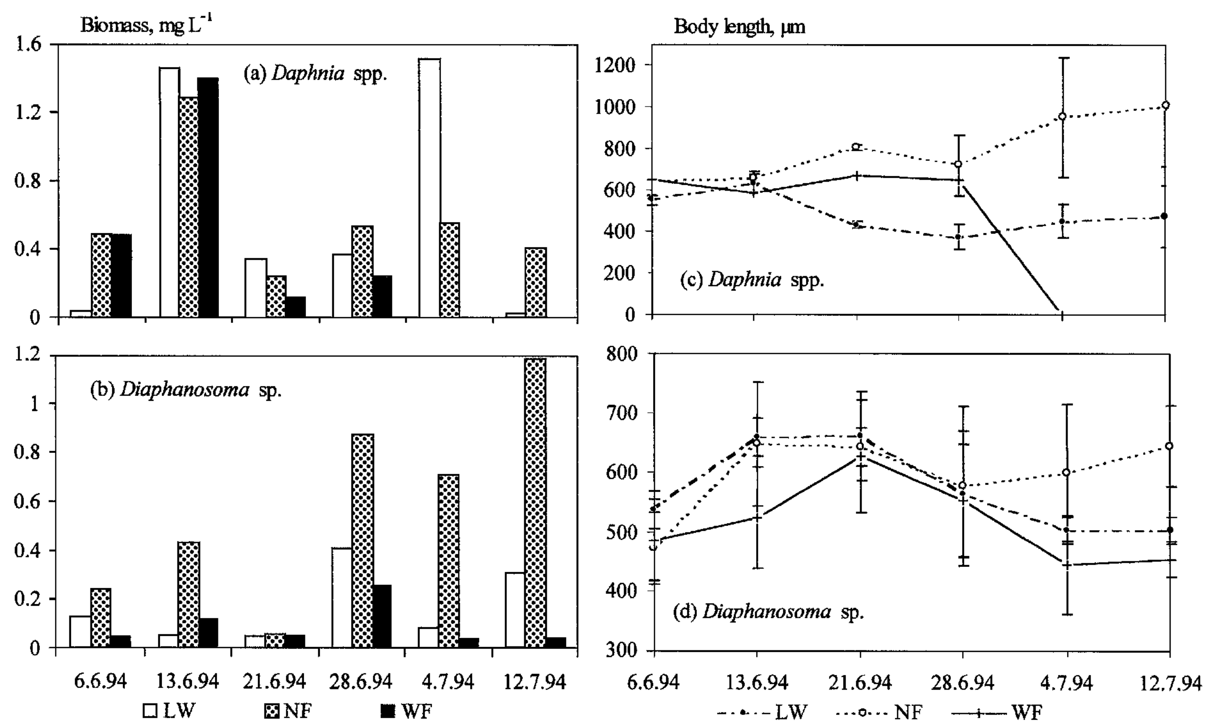


Fig. 3. Biomass and body length of *Daphnia* spp. and *Diaphanosoma* sp. in the enclosures and lakewater in June–July 1994 in Lake Feldberger Haussee.

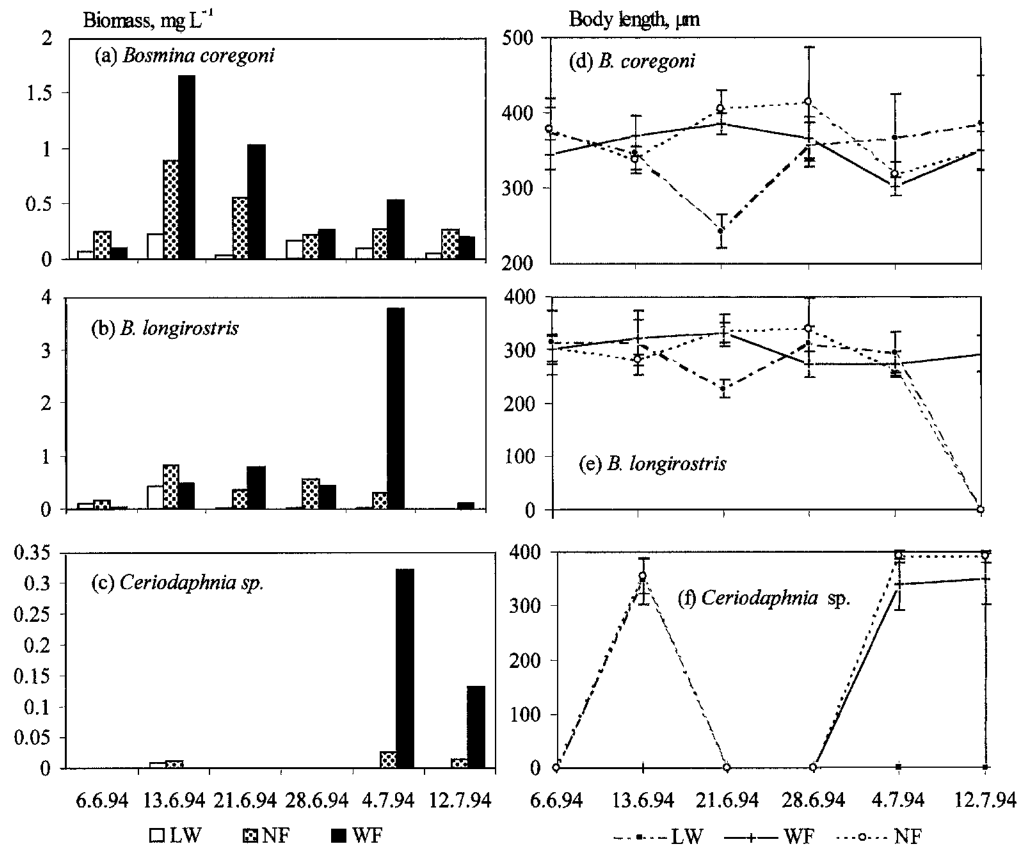


Fig. 4. Biomass and body length of *Bosmina coregoni*, *B. longirostris* and *Ceriodaphnia* sp. in the enclosures and lakewater in June–July 1994 in Lake Feldberger Haussee.

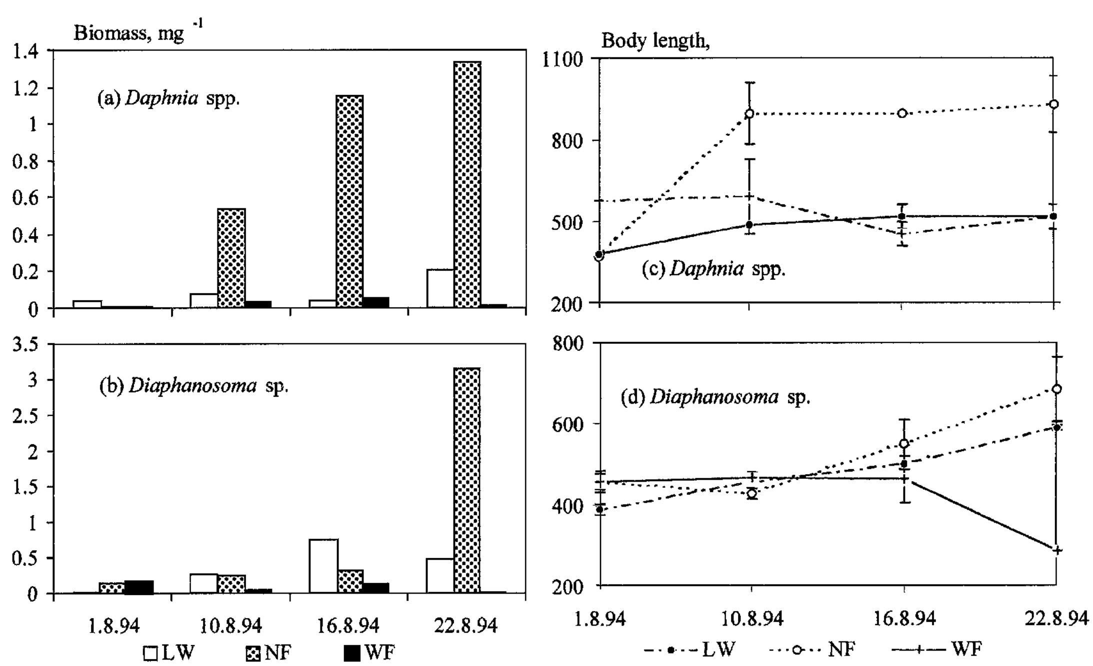


Fig. 5. Biomass and body length of *Daphnia* spp. and *Diaphanosoma* sp. in the enclosures and lakewater measured in August 1994 in Lake Feldberger Haussee.

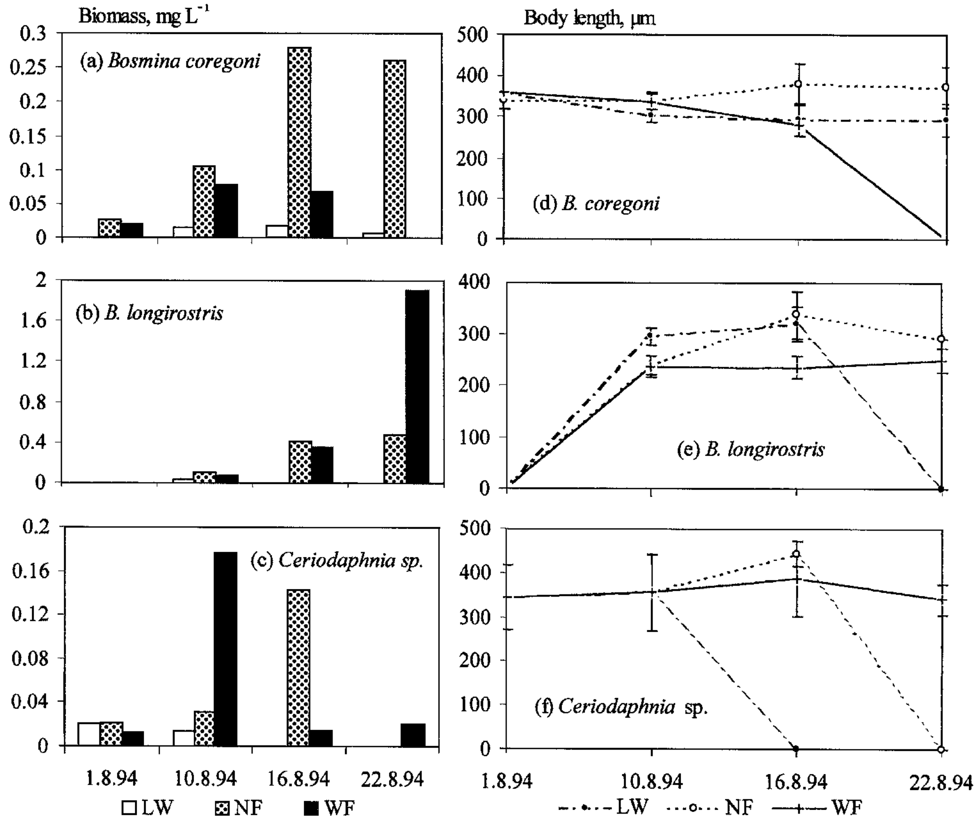


Fig. 6. Biomass and body length of *Bosmina coregoni*, *B. longirostris* and *Ceriodaphnia* sp. in the enclosures and lakewater measured in August 1994 in Lake Feldberger Haussee.

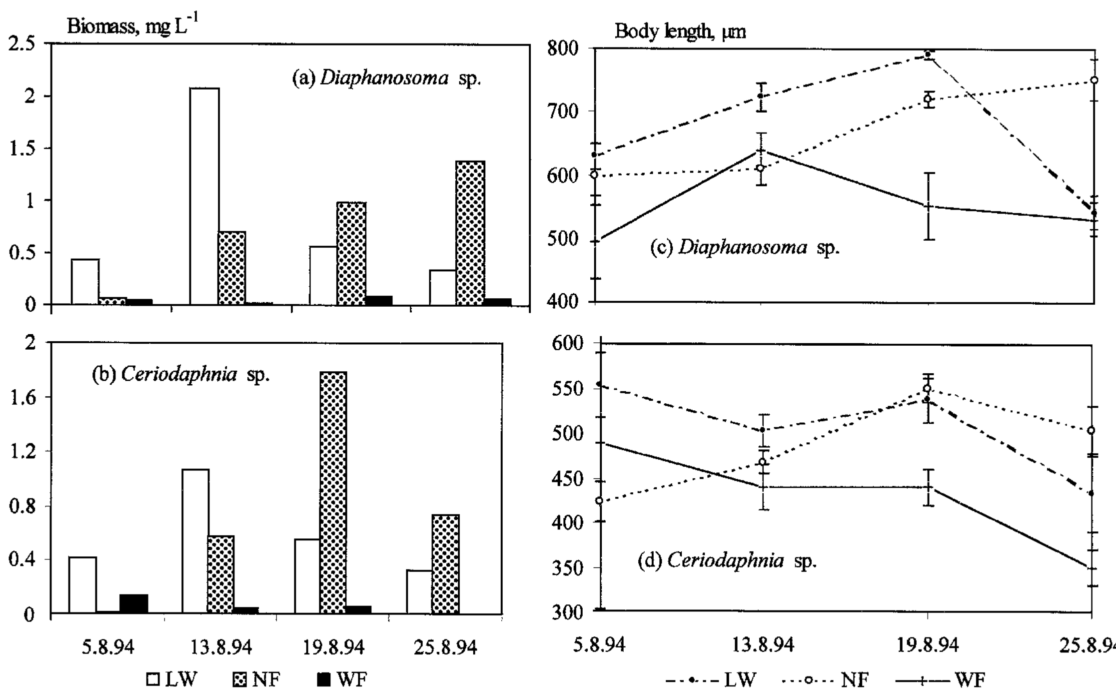


Fig. 7. Biomass and body length of *Diaphanosoma* sp. and *Ceriodaphnia* sp. in the enclosures and lakewater measured in August 1994 in Lake Große Fuchskuhle.

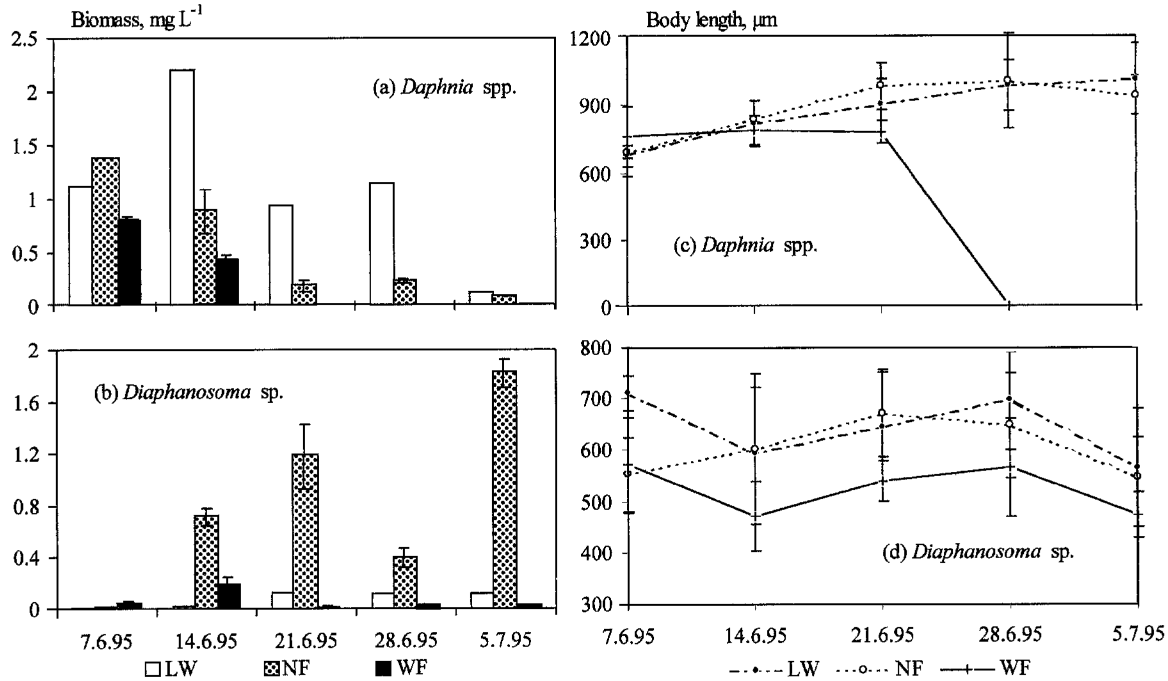


Fig. 8. Biomass and body length of *Daphnia* spp. and *Diaphanosoma* sp. in the enclosures and lakewater measured in June–July 1995 in Lake Dagowsee.

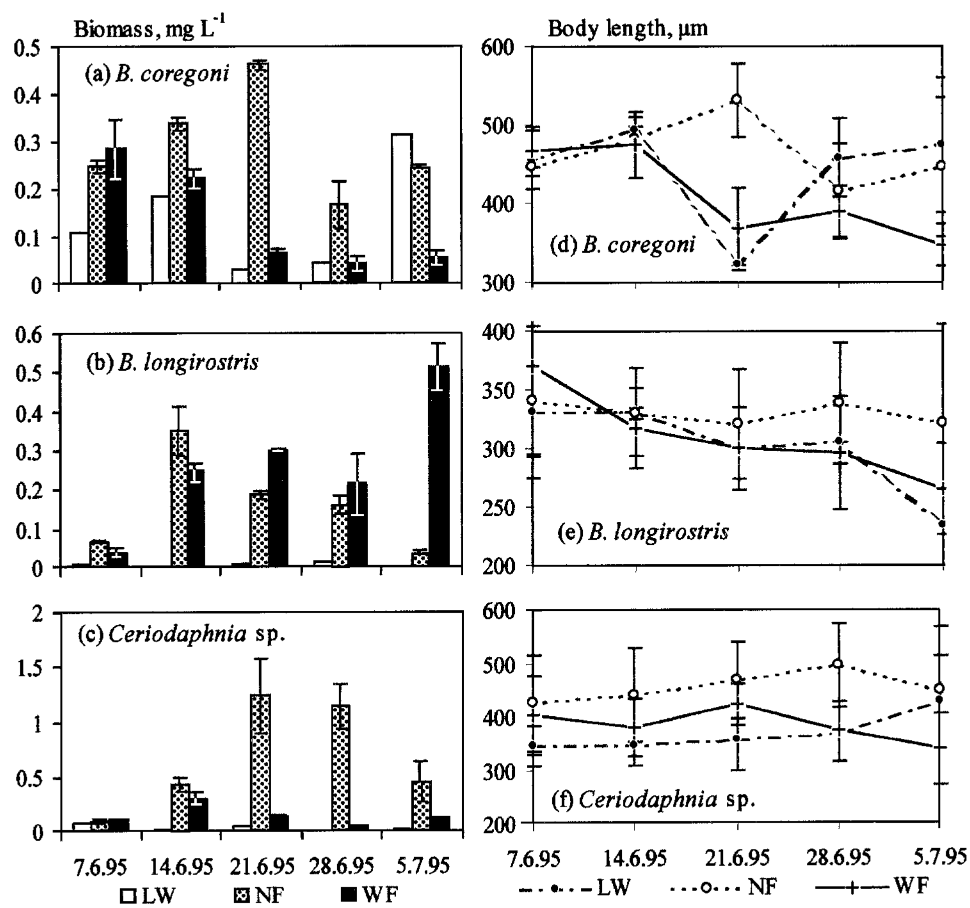


Fig. 9. Biomass and body length of *Bosmina coregoni*, *B. longirostris* and *Ceriodaphnia* sp. in the enclosures and lakewater measured in June–July 1995 in Lake Dagowsee.

more or less similar, particularly in the fish- and no-fish enclosures in biomass and body size (Fig. 4a, d). Smaller cladocerans, *Ceriodaphnia* sp. and *B. longirostris*, remained suppressed in all three systems until the last two weeks, after which their biomass increased in the fish-enclosure (Fig. 4b, c). The body sizes of these two species remained similar in the fish- and no-fish enclosures during most of the first period of experimentation. Only in the last two weeks, *Ceriodaphnia* sp. was largest in the no-fish enclosure, while *B. longirostris* was largest in the fish-enclosure (Fig. 4e, f).

The second experiment in Lake Haussee, conducted from 1.8.94 to 22.8.94, was much more pronounced in its response to vertebrate planktivory. The dominance of the cladocerans *Daphnia* spp., *Diaphanosoma* sp. and *B. coregoni* in both biomass and body size over other zooplankton in the no-fish enclosure was clearly observed (Fig. 5). The biomass of *B. logirostris* was highest in the fish-enclosure (Fig. 6b), although its body size was the largest in the no-fish enclosure as compared to their sizes in the fish-enclosure (Fig. 6e). The biomass and body size of *Ceriodaphnia* sp. remained small in the fish-enclosures (Fig. 6c, f).

Lake Fuchskuhle

The diversity of zooplankton in Lake Fuchskuhle is mainly dominated by *Diaphanosoma brachyurum, Ceriodaphnia* sp., *Eudiaptomus* sp., *Keratella* sp. and *Stentor* sp. (Table 3). There was an increase in biomass and body size of *Diaphanosoma* sp. and *Ceriodaphnia* sp. in the no-fish enclosure, while their body size and biomass decrease in the fish-enclosure (Fig. 7). The other species appeared sporadically foe very short periods. For instance, *Daphnia cucullata* appeared in negligible mass in the acidic waters of Lake Fuchskuhle disappearing in the first week of the study period. On the contrary, the ciliate *Stentor* sp. appeared in large masses in Lake Fuchskuhle. As this work was focused on cladocerans, the biomass of this ciliate and its significance on the food web is not reported here.

Lake Dagowsee

The diversity of the zooplankton structure in Lake Dagowsee seems to be similar to that of Lake Haussee (Table 3). However, the biomass of *Daphnia* spp. in Lake Dagowsee continuously decreased in all three systems lakewater, no-fish enclosure and fish-enclosure (Fig. 8a). This niche has been replaced by smaller cladocerans, namely, *Diaphanosoma* sp., *Ceriodaphnia* sp. and *Bosmina coregoni* in the no-fish enclosure (Figs. 8b and 9a, c). The biomass of *B. longirostris* decreased in the no-fish enclosures, although their body size increased (Fig. 9b & e). Despite these differences in the behavior of the different sized cladocerans in Lake Dagowsee, the body size of all species remained the largest in the absence of vertebrate planktivory as compared to those in the fish-enclosure and lakewater (Figs. 8c and 9d–f).

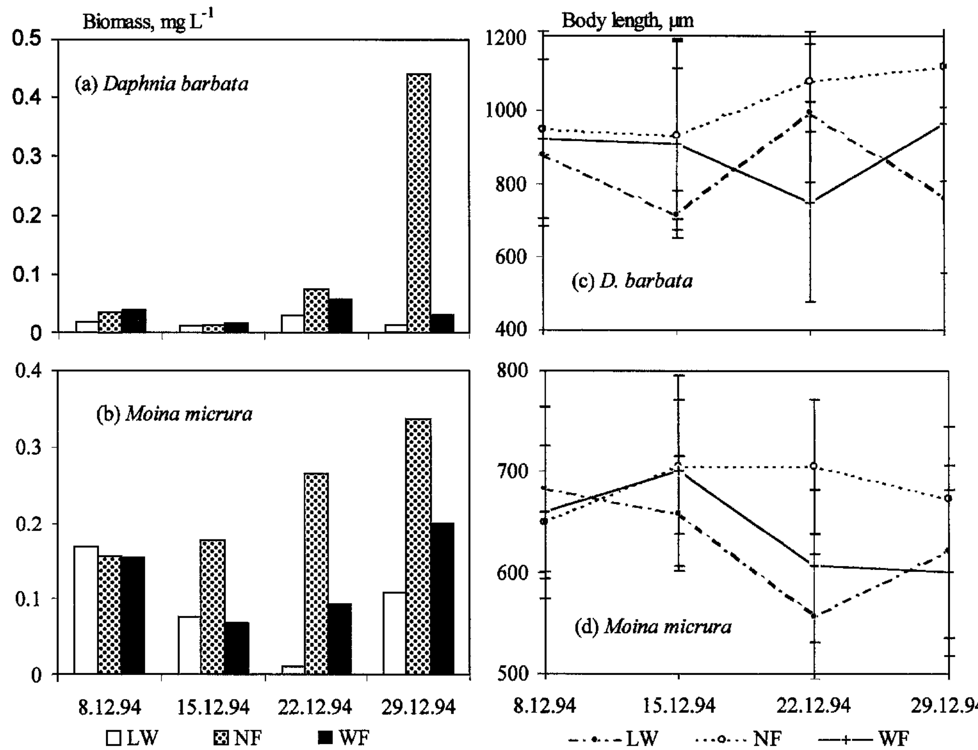


Fig. 10. Biomass and body length of *Daphnia barbata* and *Moina micrura* in the enclosures and lakewater measured in December 1994 in Lake Kuriftu.

Lake Kuriftu

In comparison to the temperate lakes described above, Lake Kuriftu in Ethiopia has lower diversity in cladoceran species and a wider range of rotifers (Table 3). Both *Daphnia barbata* and *Moina micrura* are typical tropical species. Both cladocerans proliferated in biomass and showed the highest increase in body size in the no-fish enclosure (Fig. 10). Lake Kuriftu seems to be very unique in having *D. barbata* in such biomass among tropical lakes. On the contrary, *Diaphanosoma* sp. and *Ceriodaphnia* sp. which are usually found in large masses in tropical lakes, were observed in Lake Kuriftu (Table 3) in such negligible biomass that they are not considered here.

Discussion

Data shown in Table 2 indicate that the conditions in the enclosures for the study periods were comparable to those of the lakewater. In all fish-enclosures of the four studied lakes (five experiments) different cladoceran size ranks (*Daphnia* spp., *Diaphanosoma* sp., *Ceriodaphnia* sp., *Moina micrura* or *Bosmina coregoni*, in that preferential order) were removed by fishes starting from the largest to the smallest down the size range (Figs. 3, 5, 6a, 7, 8 and 9a, c). Beyond certain size, fishes seemed not to catch small-sized individuals, mostly *B. longirostris*. That is probably the reason why *B. longirostris* thrived better in fish-enclosures than other cladocerans as observed in the four experiments conducted in German lakes (Figs. 4, 6b and 9b). Apparently, the smallness of *B. longirostris* served it as refugium to overcome fish predation. However, relatively large-sized individuals and gravid females of *B. longirostris* observed in no-fish enclosures (Figs. 6e and 9e) have not been recorded in samples from fish-enclosures. It is believed that fish removed such sizes of *B. longirostris* together with various other larger size ranges of cladoceran species. It is then likely that beyond a certain small size range of cladocerans (daphnids or bosminids), fishes tend to avoid to prey on them as there are no positive returns for the catch effort. As in SLUSARCZYK (1997) even small-sized individuals of *Daphnia* spp. (larval stages or those stunted individuals maturing earlier at small sizes) prevail in fish-enclosures protected by their small sizes. Therefore, it could be suggested that predation could be to a greater extent determined by the size of the prey of any species that brings about positive returns for the catch effort of the fishes. Of course, adults and gravid females of those species, such as *Daphnia* spp. and *Diaphanosoma* sp., are most affected by fish predation. Other species, such as *B. coregoni*, *Moina micrura*, *Ceriodaphnia* sp. are also affected by fish predation depending on the size ranges of the individuals appearing in a particular system.

The interaction of cladocerans among themselves also follows an interesting pattern. In Lake Haussee, where a wide variety of zooplankton existed in no-fish enclosures, *Daphnia* spp. and *Diaphanosoma* sp. dominated the cladoceran group by suppressing other small-bodied cladocerans (Figs. 3 and 5). A reverse situation can be observed in the fish-enclosures where zooplankton with the smallest-body sizes became dominant (Figs. 4 and 6b). In Lake Fuchskuhle, where the zooplankton assemblage is restricted, *Diaphanosoma* sp. and *Ceriodaphnia* sp. played the dominant role of the large-bodied cladocerans (Fig. 7). The acidic biotope of Lake Fuchskuhle has already excluded the small-bodied cladocerans (*Bosmina* spp.), whose place was apparently filled by rotifers such as *Keratella* sp. (BROOK LEMMA 1997). In 1995, the situation in Lake Dagowsee appeared differently, where *Daphnia* spp. proliferated during the early periods of the experiment to an unusually high population for the lake. This resulted in a sudden break in the biomass of the accessible phytoplankton size range for macrozooplankton, leaving a free niche for a sudden bloom of *Ceratium* sp. (BROOK LEMMA et al. 1996; BROOK LEMMA 1997). As a result, *Daphnia* spp. is presumed to have diminished due to starvation, leaving the niche to the next size group, namely *Diaphanosoma* sp. and *Ceriodaphnia* sp., which dominated the cladoceran assemblage in the no-fish enclosures (Fig. 8a). These species seemed to have better access to other food sources (e.g. picoplankton) than *Daphnia* sp., and hence survived the depletion in accessible phytoplankton (BROOK LEMMA 1997). Thus, first *Daphnia* spp., later *Diaphanosoma* sp. and *Ceriodaphnia* sp. where removed from the fish-enclosures, leaving a free niche for *B. longirostris* (Figs. 8 and 9c).

In Lake Kuriftu, fish and zooplankton are exposed to year-round high temperatures, illumination and continuous predator-prey interactions as described for tropical waters by FERNANDO (1994). In this tropical lake, *D. barbata* and *Moina micrura* were observed to be the dominating grazers than *Diaphanosoma* sp. and *Ceriodaphnia* sp. (Fig. 10). According to ARCIFA et al. (1986) this has probably caused the suppression of these cladocerans to a bare existence of negligible biomass in the no-fish enclosure. The fish-enclosure in Lake Kuriftu was dominated by a wide array of rotifers (BROOK LEMMA 1997) and once again by *Moina micrura*, this time represented only by small-sized individuals of its population (Figs. 10b, d). This most unusual prevalence of *D. barbata* in the tropical Lake Kuriftu offers an interesting scenario to use macrozooplankton in lake restoration practices in the tropics, where lakewater is used for household purposes including direct consumption by the rural community, animal watering, irrigation, bathing, washing clothes and recreation.

Based on these observations, it may be suggested that the size factor has apparently played an important role in vertebrate planktivory and cladoceran relations. The size efficiency hypothesis seemed to be at work in these experiments, whether the dominating species is *Daphnia cucullata*, *D. barbata*, *Diaphanosoma* sp. or *Moina micrura* as described in CARPENTER et al. (1985), KERFOOT & SIH (1987), BENNDORF (1988), GULATI et al. (1990), CARPENTER (1988) and GLIWICZ (1994).

The interactions of cladocerans among themselves are also observed in one tropical and three temperate lakes. This case suggests that the competitive exclusion theory seems to be operating as described by LAMPERT & SOMMER (1993), BEGON et al. (1996) and others.

It was also observed that the dominance of *Daphnia* spp. couldn't be brought about by the absence of planktivory or prevented by the presence of fish predation alone. The appearance of *Daphnia* spp. could (a) be assisted by the availability of refuge such as high turbidity when planktivory prevailed in Lake Kuriftu, (b) prevented by lakewater acidity when fish predation was removed in Lake Fuchskuhle, or (c) broken-down when inaccessible phytoplankton dominate in Lake Dagowsee. The case of Lake Haussee also adds to the complexities that even when *Daphnia* spp. dominate in the absence of fish predation, there was still an excess of accessible phytoplankton (see KRIENITZ et al. 1996; BROOK LEMMA 1997). These scenarios of biomanipulation may be used in all lakes as an instrument of lake restoration. The possibility of using a combination of methods, based on interdisciplinary approach still needs further work.

One last observation that probably deserves a short discussion is the behavior of *Ceriodaphnia* sp. in the whole scenario of interactions among cladocerans. This species seemed to appear in appreciable biomass only when the domination of *Daphnia* spp. was hindered, either by an acidic biotope as in Lake Fuchskuhle or starvation as in Lake Dagowsee (Figs. 7b, 8a and 9c) or for no apparent reason as in Lake Haussee (Figs. 3a, b and 4c). *Ceriodaphnia* sp. also seems to have been challenged by the domination of *Diaphanosoma* sp. during the decline of *Daphnia* spp. in Lake Haussee and Lake Dagowsee in the last weeks of experimentation. Thus further verification may be needed if there is a sharp or *complete competitive exclusion* (a term defined by JACKSON & JACKSON 1996) between *Ceriodaphnia* sp. and *Daphnia* spp. or *Diaphanosoma* sp. in no-fish scenarios. It may then be said that complete competitive exclusion might have lead each time to *Daphnia* spp. domination, with *Ceriodaphnia* sp. awaiting the elimination of Daphnids by some means other than fish predation. This of course requires further study.

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